

A phylogenetically interesting sphaeriodesmid milliped from Oaxaca, Mexico (Polydesmida: Sphaeriodesmidae)

by

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With 15 figures

ABSTRACT

Proellodesmus mecistonyx is described as a new genus and species of Sphaeriodesmidae, from a single specimen taken in a cave in north-eastern Oaxaca. The species is remarkable in that several character systems, upon the derived state of which the family has been diagnosed, are represented by the generalized condition producing, in effect, a sphaeriodesmid not completely modified for rolling into a sphere. The concurrence of these exceptional plesiomorphies creates a possible model for an ancestral level stage in the sphaeriodesmid clade. The opportunity afforded by description of this animal is taken to review the postulated affinities of the families Sphaeriodesmidae and Holistophallidae, in the light of a species which partly bridges the hitherto substantial hiatus between the two.

INTRODUCTION

Recently I received, through the kindness of Professor J. M. Demange (Muséum National d'Histoire naturelle, Paris) a small collection of millipeds from Mesamerican caves, included amongst material sent to him for identification by M. Villy Aellen, Director of the Muséum d'Histoire naturelle, Genève. As is often the case with cave material picked up incidentally, most of the specimens thus coming to my hand were females and immatures, but one vial commanded attention as at first glance it appeared to contain a large male pterodesmine cryptodesmid. Examination replaced one surprise with another and greater: the specimen proved to be a sphaeriodesmid, but one not

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modified for volvation! Despite this apparent contradiction in terms, there can be no doubt, as will be made clear in subsequent drawings and descriptions, that the animal embodies enough basic characters of the Sphaeriodesmidae that no other placement can be defended. Concomittantly, the family definition obviously must be modified to accommodate this new and disjunct member. In fact, one might even justly use the term "charter member" in a phylogenetic sense, as the species has obviously retained, in many facets of its body form, the image of what the ancestor of modern sphaeriodesmids may have looked like.

I wish to express at this point my best thanks to Professor Demange and Professor Aellen for the opportunity to study one of the most interesting diplopods that has come before me in many years. The advantage of his familiarity with sphaeriodesmids ensured authoritative review of an early draft of the manuscript by Dr. William A. Shear.

Family Sphaeriodesmidae

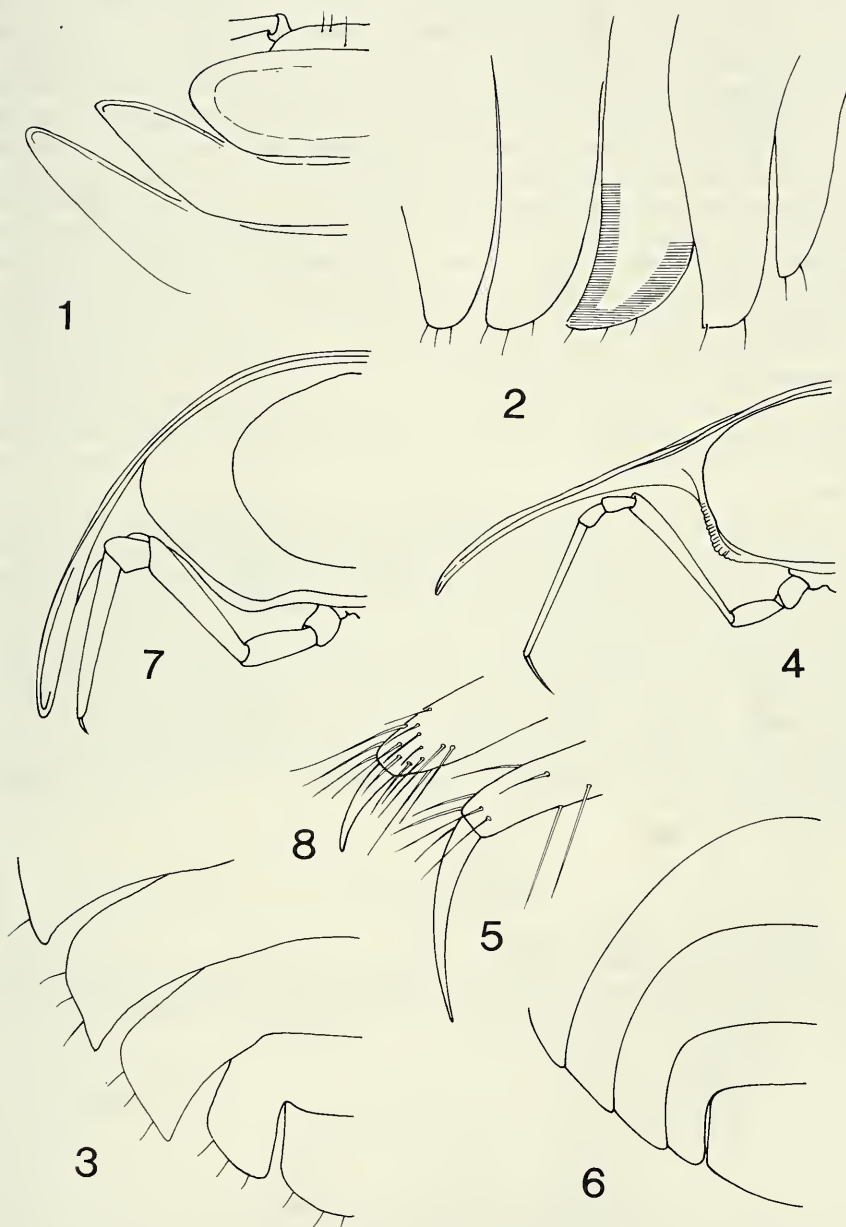
In its present context, the Sphaeriodesmidae contains about 90 nominal species organized into 15 genera and three subfamilies. Although outlying species occur in eastern United States, Panama, and the West Indies, the metropolis of the family is clearly in southern Mexico and Guatemala, which are inhabited by dozens of species referable to the nuclear genus *Sphaeriodesmus* in its present, very inclusive sense. In commenting on this melange, SHEAR (1986: 81) has noted fantastic diversity in gonopod structure despite essential identity of body form among its components (eventual resolution of this "genus" into smaller and more homogenous taxa is almost inevitable).

The relationship of the family to other volvant polydesmidans is reviewed briefly in a concluding essay. For the immediate context, it can be noted that its internal classification is by no means satisfactory and will not be until a painstaking revision of all known (and a host of still undescribed) species can be accomplished. The most recent arrangement (HOFFMAN, 1980) proffers three subfamilies, Sphaeriodesminae, Desmoninae, and Bonetesminae, probably a far-too conservative concept. Possibly cyclodesmines, presently merged into the nominate subfamily, warrant restoration to some level of recognition, and quite likely *Bonetesmus* represents disjunction of family-group importance. In some ways, the new genus described here is different enough from all of the foregoing to require higher category status. I believe however, that pending comprehensive revisionary study, a moratorium can be invoked against piecemeal alterations. In particular, a reevaluation of the structure of *Cyclodesmus*, based on fresh topotypic material, would appear to be of primary importance.

FIGS 1-8.

Structural details, *Proeilodesmus* and *Sphaeriodesmus*.

Figs 1-5: *Proeilodesmus mecistonyx*, n. sp. — 1: Epicranium and first three body segment, left side, dorsal aspect. — 2: Right paranota of segments 2-6, lateral aspect, with distribution of surface striation indicated in part on segment 4. — 3: Left side of segments 17-20, dorsal aspect, separation of paranota represents natural condition and not the result of flattening. — 4: Posterior view of left side of midbody segment, showing extreme elongation of paranota (much greater than diameter of body cavity) and shape of legs. — 5: Tarsal claw of midbody leg. — Figs 6-8: *Sphaeriodesmus neglectus* Carl. — 6: Left side of segments 17-20, posterodorsal aspect, showing compaction of segments typical of sphaeriodesmids generally. — 7: Posterior aspect of left side of midbody segment, showing proportions and paranota and legs, for contrast with Fig. 4. — 8: Tarsal claw of midbody leg. All figures drawn X15 except 5 and 8, X90.



The large number of species and frequent abundance of individuals suggest that the ability to enroll into a compact sphere conferred a distinct advantage on these animals. Under its security, they seem to have accepted the constraints of a successful body plan and specific differentiation is largely limited to secondary sexual characters (where, to be sure, it is indulged with a vengeance). Volvation has been adopted by a number of millipeds (glomerids, sphaerotheriids, sphaeriodesmids, cryptodesmids, oniscodesmids, and doratodesmids) as well as terrestrial isopods, all utilizing variations on a few basic structural modifications. Generally the dorsum is arched and its convexity is continued ventrad by distally narrowed paranota or comparable tergal extensions; the ultimate tergum (telson, epiproct) is broadened and flattened; the last five or six segments tend to be reduced and notably compacted; and one or two of the anteriormost terga (2nd-5th) are laterally expanded and provide a circular basis against which the apices of other terga abut during volvation. In glomerids, sphaerotheriids, and oniscoid isopods, the effect produced is that of a sphere; in polydesmoids the form is of a flattened sphere or disk.

To enhance enrolling, most segmental prozona are strongly reduced, and metasterna just large enough to accommodate the coxal sockets. Ozopores tend to be very small or lost entirely. Even though most sphaeriodesmids (and other polydesmidan volvants) are epigaeic, they have forsaken the almost universal ordinal trait of bright color patterns and are uniformly white, gray or testaceous beneath the usual surface coating of soil particles.

An impression of the tergal modifications in sphaeriodesmids may be gained by inspection of figures 6 and 7, drawn from *S. neglectus* Carl, a fairly representative species. All members of the family have the same general body form (aside which anterior paranota are enlarged), and even though they have obviously evolved from some kind of "normal" polydesmidan ancestor, heretofore no approximation of that prototype was known to be extinct or fossilized. Now *Proeilodesmus* goes a long way to bridging the gap. But in addition to retention of some obvious plesiomorphies, the genus has developed a few innovations peculiar to itself, perhaps the result of adaptation to cave life. It is interesting to speculate that, in becoming a troglobiont at some remote time, the organism may have escaped whatever selective pressures provided the option of volvation to its epigaeic relatives.

***Proeilodesmus* gen. nov.**

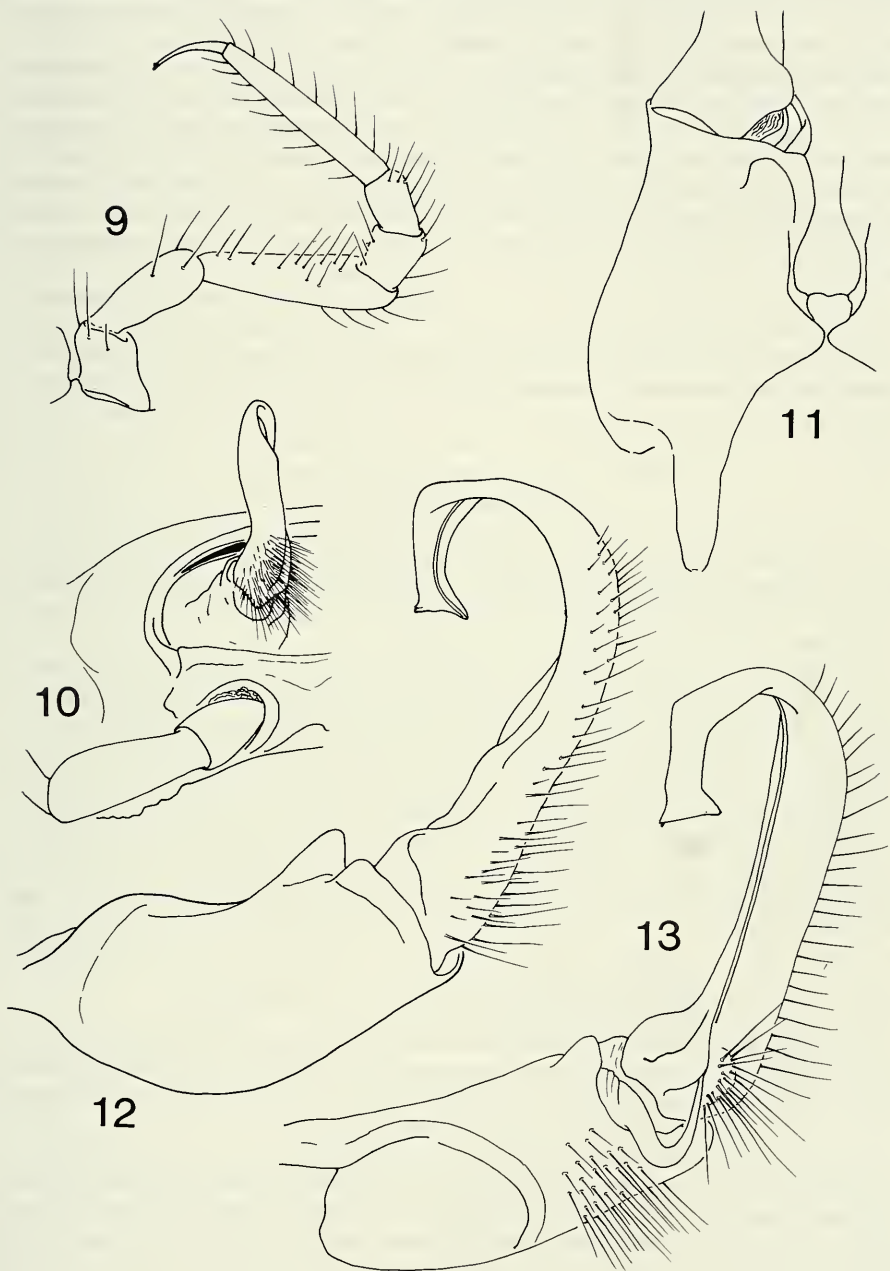
Type species: *P. mecistonyx*, sp. nov.

Diagnosis: A sphaeriodesmid genus with the following distinctive characters: labrum with five small median teeth; anterior paranota only slightly modified, 4th slightly larger than others, 3rd and 5th subequal; paranota of mid-body segments remarkably wide and

FIGS 9-13.

Secondary sexual characters, *Proeilodesmus*.

Fig. 9. — Right leg of first pair of male, aboral aspect, showing elongated and totally unmodified podomeres. — 10: Right side of 7th segment, ventral aspect, showing gonopod *in situ*. — 11: Coxa and base of telopodite of left gonopod, dorsal aspect, showing mesal parasternal lobes, and sternum (stippled). — 12: Right gonopod, lateral view. — 13: Left gonopod, mesal view. Figs 9 and 10 drawn X15, 11-13 X90.



only slightly deflexed ventrad (Fig. 4), the apices only slightly exceeding level of sterna; paranota of posteriormost segments overlapping only at base; lateral edges of all paranota with three setae; tarsal claw as long as prefemur (twice as long as in sphaeriodesmids of equal size); all legs, including first pair, remarkably long and slender.

Gonopods (Figs 10-13) of typical sphaeriodesmid form. Coxae dorsoventrally compressed, with small supracannular apophysis, a small median sternal remnant present, but coxae also in contact through large medially projecting lobes near base of apodemes; paracannular setal field present. Telopodite attached at about 45° angle, prefemoral region elongate, only slightly enlarged proximally, distal third of telopodite recurved proximomedially through just over a half-circle; prostatic groove mostly visible in mesal aspect. First pair of legs long and slender, without modifications. Characters of female unknown.

Distribution: Known only from the type locality of the single included species, in northeastern Oaxaca, Mexico.

Name: Composed of the greek terms *pro* – (in the sense of early or antecedent) + *eilos* (able to roll up) + *-desmus*, a common suffix used in this order; literally meaning a sphaeriodesmid not yet able to enroll.

***Proeilodesmus mecistonyx* sp. nov.**

Figures 1-5, 9-13

Material: Male holotype (Mus. Genève), from the cave "Nita Diplodocus" at Cerro Rabon, northeast of Huautla de Jimenez, Oaxaca, Mexico; U. Widmer and Philippe Rouiller leg. (Cerro Rabon Project), 21 March 1987. Cf. JEANNIN, 1987.

Diagnosis: With the characters of the genus.

Holotype: Adult male, body at present fragmented but approximately 24 mm in length, widths of selected metaterga as follows: 1-4.0 mm; 2-6.1 mm; 3-8.0 mm; 4-9.3 mm; 6-9.5 mm; 8-9.7 mm; 12-9.6 mm; 14.9.3 mm; 16-8.3 mm; 18-6.0 mm.

Surface of head smooth and polished; labrum slightly prolonged ventrad with a vague labroclypeal offset each side, median labral notch with five equal-sized small teeth. 2-2 epicranial setae, 1-1 interantennal setae, frontal setae sparse, numerous and irregular, lower labral setae about 10-10, upper series about 6-6, each set in a distinct fovea. Interantennal isthmus broad. Epicranial suture distinct but not impressed. Antennae long and slender, articles in decreasing length order 2 = 3 = 5 > 6 > 4; articles 5 and 6 with small distal field of short sensory setae, four terminal sensory cones; setation uniform and sparse, setae about as long as basal diameter of each article. Surface of gnathochiliarium essentially glabrous. Mandibles larger than normal for sphaeriodesmids, and individual filaments of the pectinate lamellae longer.

Collum (Fig. 1) transversely-ellipsoidal, nearly flat, anterior edge slightly bisinuate, posterior edge evenly arcuate, forming obtuse angle with anterior at lateral ends; anterior edge with fine but distinct margin, and a single short seta at each end; a submarginal transverse row of 3-3 longer setae in front of posterior edge.

Second segment transverse, its paranota directed anteriorly and evenly acuminate to lateral apices, only outermost smooth, median areas slightly convex, all margins compressed and flattened. Four marginal setae at each end, and two transverse series of hairs middorsally, about 6-6 medially and ca. 12-12 near posterior edge. Third segment much larger than second, paranota broader and about the outer half decurved; surface as described for 2nd, apical setae reduced to one or two at each end, and middorsal series also reduced. Subsequent segments with paranota increasingly deflected ventrad (shape of

anterior paranota, Fig. 2) and prozona more strongly developed, becoming about half as long as metazona middorsally. Anterior rim of paranota continued directly across dorsum as posterior edge of prozona.

Paranota laterally acuminate and subacutely rounded back to about 9th segment, thereafter becoming more truncated and increasing in length; by 14th segment an angular posterior corner is developed. Anterior edges smooth, posterior minutely granulose-denticulate. Form of posterior paranota (Fig. 3).

Epiproct broad, truncate, galeate, the two pairs of apical setae displaced to the underside of the median rim. Two other pairs of setae remain on the edge. Paraprocts smooth and shiny, indistinctly divided by an oblique depression, no well-defined mesal rims evident. Hypoproct large, in the form of an equilateral triangle with rounded angles, its length about equal to exposed commissure of paraprocts, its surface smooth and nearly flat; paramedian setae small, set on edge.

Podosterna small, slightly elevated, with transverse impression, narrow, intercoxal space about a third of coxal length, decreasing gradually posteriad until coxae of last pair are in contact. Prozona narrowed ventrad, almost obliterated midventrally but produced into low blunt lobe on each side just above base of anterior legs. Sides of metazona smooth, notably flared posteriad just laterad to coxal base. Stigmata unusually small, forming minute subpyriform tubercles atop each coxal condyle. Legs (Fig. 4) very long and slender, femora and tarsi especially elongated, all podomeres sparsely set with long setae; tarsal claws (Fig. 5) twice length normal for the family, even on 1st pair of legs.

Anterior legs and sterna unmodified, legs of 1st pair (Fig. 9) without trace of femoral gland or process. Gonopod aperture small and oval (Fig. 10), posterior edge produced into an elevated thickened rim. Gonopods (Figs 11-13) as described in the generic heading, of the basic generalized sphaeriodesmoid form.

Remarks: Attention is directed to an unusual structural feature not observed by me in other diplopods although perhaps overlooked. As roughly indicated in Fig. 2, the periphery of each paranotum of *Proeilodesmus*, as seen with low magnification, appears to be very finely longitudinally striated. The "striations" extend quite to the caudal edge in all cases, but appear not to attain the anterior edge because of the abrupt upturn of the anterior margin. In fact the "striations", as can be seen when the paranota are backlighted, are really fine internal tubules which originate with the parenchymatous internal core of the paranota and extend to the surface on the entire periphery. If not secretory in nature, I cannot imagine what the function of such a pervasive system might be.

Commentary on the superfamily Sphaeriodesmoidea

As implied in the group name, sphaeriodesmids have specialized in volvation and their structure represents a suite of concomittant apomorphies. Heretofore the affinities of the family have been only marginally addressed, and a definite position has yet to be established.

In his first attempt at classification of polydesmidans, O. F. COOK (1895) admitted the single family Oniscodesmidae (with the genera *Cyphodesmus*, *Oniscodesmus*, and *Sphaeriodesmus*) to include the volvating taxa then known to him. Only a short time later, he (COOK 1896: 28) recognized four families: Oniscodesmidae, Cyclodesmidae, Cyrtodesmidae, and Doratodesmidae for volvant species without making any useful contrasts between them and with only the remark that *Oniscodesmus* showed "a very evident relationship to the Pterodesmidae [a cryptodesmoid group not adapted for

volvation].” In his definitive paper of 1898, after the examination of many pertinent species, COOK noted that the ability to enroll the body had probably evolved independently at least three times within the Polydesmida, and defined five families to reflect this popular convergence. Most of Cook’s distinctions were based on details of body form, and although the monophyly of his taxa can hardly be disputed, he offered no insights on their affinities with other families of the order.

Appearing during the same year, ATTEMS’ first classification of polydesmidans (1898: 266) recognized three coordinate groups Cyrtodesminae, Oniscodesminae, and Sphaeriodesminae, the first containing *Cyrtodesmus* and *Doratodesmus* (amongst others), the second embraced *Oniscodesmus* and four other genera, and the third was composed of *Cyclodesmus*, *Sphaeriodesmus*, and *Cyphodesmus*. It was not a bad arrangement for the time, but curiously, in the main textual accounts of these groups appearing in the next year (ATTEMS 1899: 378-392) the first two subfamilies were combined under *Oniscodesmus* without a word of explanation.

R. I. POCK (1909) followed the precedents set by COOK and accepted his 1898 classification except for reducing Cyrtodesmidae and Cyclodesmidae to subfamily status under Oniscodesmidae and Sphaeriodesmidae respectively. Pocock also supported the view (credited to Brolemann) that sphaeriodesmidids might be related to chelodesmidids whereas oniscodesmidids were possibly derived from the polydesmidid group. However, in his magisterial classification of polydesmidans BROLEMANN (1916) did not develop such lines of affinity, and grouped all volvating species into the single family Oniscodesmidae which was divided into Oniscodesminae and Sphaeriodesminae. Referring to this family in its broad sense, BROLEMANN (1916: 559) noted that the gonopods were basically the same as in chelodesmidids, which is, however, strictly true only for the sphaeriodesmidid components. In his 1916 “Essai” BROLEMANN did not speculate on the actual relationships of these taxa, aside from ranking the Oniscodesmidae in his suborder Leptodesmida. Brolemann’s disposition was accepted in toto by ATTEMS in the organization of the Polydesmida as he treated it in 1938-40. A step backward was taken by VERHOEFF in 1941, who suggested the Oniscodesmidae and Sphaeriodesmidae be placed in a new suborder Sphaerosomita (an exaltation of parallel evolution!).

The most recent consideration of the situation was embodied in my recent (HOFFMAN 1980) “Classification of the Diplopoda” in which sphaeriodesmidids are retained in the suborder Chelodesmida in close association with the Holistophallidae, whilst the other families (Oniscodesmidae, Cyrtodesmidae, Doratodesmidae) are placed at various locations within the Polydesmida. Owing to space constraints, no extended documentation was provided, but a few points were adduced to justify union of sphaeriodesmidids and holistophallids in the same superfamily.

Present knowledge of *Proeilodesmus* permits renewed attention to this latter relationship as well as, of course, position of the genus within the phylogeny of sphaeriodesmidids.

Although the Sphaeriodesmidae is a familiar taxon, frequently treated in taxonomic literature, the Holistophallidae remains little-known and under-appreciated. Originally proposed in 1909 to contain only its monotypic type genus, the family was absorbed into the Rhachodesmidae by BROLEMANN (1916) and by ATTEMS (1926, 1940), and did not emerge with a separate identity until the appearance of the checklist of Mesamerican millipeds (LOOMIS, 1968) which admitted the Holistophallidae with no fewer than seven genera. During the early 1960’s, the family had come under scrutiny and considerable revisionary work (unfortunately still incomplete) was accomplished. The main characters were worked out and several genera placed in the Rhachodesmidae were re-allocated for the list which I provided Mr. Loomis.

The major diagnostic features of the family include: 1. drastic displacement of the stigmata from the normal supracoxal location to a new position in the stricture (or even into the prozonum!), 2. development of large, horizontal paranota which are unusually thin toward the edges with only minimal peritrematic expansion, 3. the occurrence of prominent tarsal scopulae on legs 1-5 of males in most if not all genera. The body form adheres closely to a basic groundplan in all known species (about a dozen described, an equal number still unpublished), but male genitalia display an astonishing diversity ranging from perfectly "normal" chelodesmoid patterns to prodigies of condensation in which only a monarticular remnant persists. Except for this monotonous fidelity in body form despite all these gonopodal permutations one could, in consistency with the standards of other families, set up a new family for nearly every holistophallid genus.

In proposing a superfamily to include both holistophallids and sphaeriodesmids (HOFFMAN, 1980), I turned for justification to two points: one being shared form of the gonapophyses (very long, slender, and tubular), the other the remarkable similarity of gonopod structure in several holistophallid and sphaeriodesmid genera. *Tunodesmus* was cited as an example of this character, and it is appropriate at this time to present tangible verification. The gonopod drawings given in the original description of *Tunodesmus* (CHAMBERLIN, 1922) show only the gonopods *in situ*, which reveals a minimum of information. I give here (Fig. 14) an illustration of the left gonopod of *T. orthogonus* made from mesal aspect, and believe that any systematist familiar with sphaeriodesmids would readily accept this drawing as one made from a species related, e.g., to *S. iglesia* SHEAR (1986: fig. 40) or *S. neglectus* CARL (1902: fig. 107). The body of the animal, of course, is endowed with the usual holistophallid attributes and could not possibly be mistaken for anything else. Species of other holistophallid genera, moreover, have gonopod telopodites of a simpler formation, comparable to sphaeriodesmids of the *S. mexicanus* group.

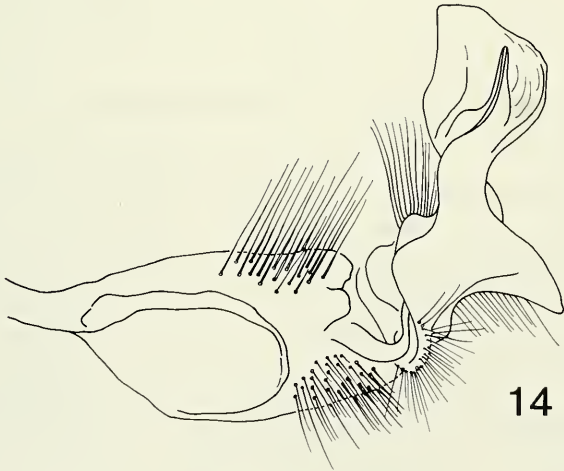


FIG. 14.

Tunodesmus orthogonus Chamberlin, left gonopod of male holotype to show overall similarity in proportions and setation with the gonopods of many species of sphaeriodesmids.

As already noticed in a preceding heading, the gonopods of *Proeliodesmus* adhere closely to a simple generalized form (Figs 11-13) such as occurs in many species of *Sphaeriodesmus*. While there is no evidence that even such flagrant plesiomorphy as the body form of *Proeilodesmus* correlates with the polarity of any other character system, perhaps it is justifiable to suppose as did SHEAR (1986: 82) that the simpler telopodite structure may be generalized within *Sphaeriodesmus*. If so, it could be construed as a symplesiomorphy of that genus, *Proeilodesmus*, and the Holistophallidae, antedating the divergence of the two families as do also the synapomorphic gonapophyses.

The fact that the range of Holistophallidae coincides with the area of greatest diversity of sphaeriodesmoids is instructive and suggests that the two originated from some common ancestor in the same general region, possibly during an archipelagic phase of Mesamerican landscape (perhaps along with the present-day Rhachodesmidae).

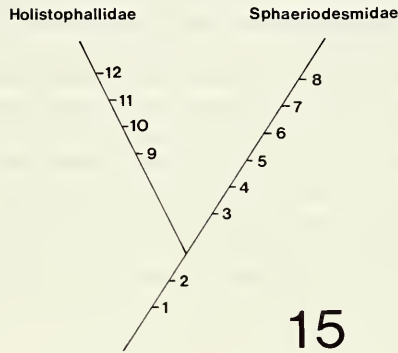


TABLE 1.

Character states in the Sphaeriodesmoidea

Character	Plesiomorphic state	Apomorphic state
Gonocoxal setation	Sparse, irregular, absent	1. Profuse fields
Gonapophyses	Absent or small	2. Long, tubular
Prozonal size	Equal to metazona	3. Greatly reduced
Ozopores	Present	4. Reduced or absent
Paranotal shape	Normal for order	5. Strongly acuminate laterad
Shape of epiproct	Subtriangular, acute	6. Quadrate, broadened
Size of stigmata	Normal for order	7. Reduced, circular
Anterior paranotal shape	None evidently enlarged	8. 4th & 5th enlarged
Location of stigmata	Normal position	9. Displaced into stricture
Subtarsal scopulae, male legs	Absent	10. Present, legs 1-7
Gonosternum	Present	11. Absent
Shape of gonaperture	Oval, moderate in size	12. Reduced or enlarged

To encapsulate the foregoing commentary in the form of a cladogram, I provide the following summary of important characters and their relative polarity, the numbers corresponding to those entered on the tree itself (Fig. 15). As usual, estimation of generalized versus derived status has been done chiefly from "out-group" comparison. Since current knowledge of milliped classification does not permit identification of a "sister-group" taxon of equivalent rank to the Sphaeriodesmoidea, the out-group has been the chelodesmoid families perceived to be basically unspecialized, e.g., Chelodesmidae, Xystodesmidae, Oxydesmidae collectively. No clues are presently available from the area of ontogenic changes.

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